

Avian zoogeography, speciation and the museum tradition

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SUMMARY

Zoogeographical studies involving the identification of speciation patterns in birds have been greatly facilitated by the preparation of distribution maps using published localities and unpublished museum specimen records. Zoogeographical patterns in Amazonian birds include six conspicuous areas of endemism and numerous sharply defined contact zones between closely related geographically representative birds. Many contact zones cluster along the Amazon and the lower portions of its tributaries, but others cross river courses at rightangles. Parapatric contact zones generate many important riddles over the processes whereby species remain intact (do the zones remain stationary or fluctuate, how is parapatry maintained, why and when did it originate? etc.); parapatric patterns in New Guinea lowland birds offer further opportunities to solve such questions. Studies based on museum collections continue to contribute valuable data on the character geography of particular species groups (in the case of migrant Arctic waders based on extensive quantification of subtle character differences between populations), on geographical variation of sexual dimorphism, and geographically variable polymorphism.

Introduction

Bird collections in natural history museums document the occurrence of common, rare, threatened and extinct species obtained in accessible and inaccessible areas of the world. Collections form the basis of systematic and zoogeographic studies, for research on geographic variation, study of plumage colour patterns, ecomorphology, biodiversity and many other topics. Early private and public collections were already important during the period when ornithology originated as a separate branch of zoology during the first half of the nineteenth century. Later, scientists and commercial collectors travelled widely overseas contributing to the rapid growth of the regional knowledge of the avifaunas of the world, and leading to a conspicuous boom in bird collections during the second half the nineteenth century and into the twentieth century (Stresemann 1975, Barrow 1998, Mearns & Mearns 1998, Haffer 2001, Glaubrecht 2002).

Below I demonstrate the constant and non-substitutable relevance of museum collections to the topic of avian zoogeography, in particular the mapping of breeding and wintering ranges of birds, the study of individual and geographic variation, the analysis of contact zones between subspecies and species as well as of areas of endemism. I show that bird collections stored in museums are essential tools for such research. Conceptual contributions of systematists to biological science through specimen-based research include the theory of geographical speciation, the principle of population thinking, and the interpretation of the gradualness of evolution.

Mapping of breeding and wintering ranges

Precise locality data and the dates of collecting are the basic information on specimen labels needed for taxonomic and zoogeographic work. Such notes are often supplemented by data on the colour of bill, feet, iris and skin around the eye, as well as by information on moult and stomach contents. The field notebooks of the collectors frequently provide information on the ecology and calls of particular birds. Obviously, the correct labelling of museum specimens, as to where and when a bird was taken, is of crucial importance, including information on the altitude of the collecting locality, especially in mountains, and its position with respect to the left or right bank of a broad river. Occasional misidentifications of birds can only be clarified through reference to preserved specimens.

Locality data are utilised in taxonomic and faunistic publications as well as in regional atlas projects like those which have been published for Palearctic and African birds. In the Palearctic atlas (Stresemann, Portenko *et al.* 1960–2000) the limits of the breeding ranges of selected species are mapped and the localities used to trace these range limits are documented in the accompanying text of each map, which also includes discussions of the ecology and taxonomy of these birds. The detailed documentation of all localities as to their literature source permits their verification in case of later need. So far 19 instalments of this atlas treat 210 species of birds in 62 genera which have been studied cooperatively by 16 scientists, mainly at the Berlin and St. Petersburg Zoological Museums.

The atlases of African passerine (Hall & Moreau 1970) and non-passerine birds (Snow 1978) map the distributions of more or less related and geographically representative species onto a background vegetation map of Africa. Each locality where a species has been collected is marked with a particular symbol (solid or open circle, triangle, square, etc.). Such presentation permits at-a-glance appreciation of the ecological occurrence of a species, its relative abundance (few or many locality records) and the location of contact zones, i.e. areas of geographic replacement, between related representatives (with or without hybridisation). These aspects would not be so obvious if the distribution of each member species of such superspecies or species groups had been illustrated on a separate map. Numerous opportunities for field studies become apparent simply by studying these African maps.

Although the use of point-locality mapping in these African atlases is extremely valuable as a means of establishing baseline distributions, there are two drawbacks (N. J. Collar pers. comm.): (1) the mapped locality records are not tagged with a source, so that in cases of doubt they cannot be scrutinised; and (2) not all sources have been used and certain information is missing. In a less detailed manner, Moreau (1972) mapped and discussed the summer and winter distributions of all Palearctic migratory birds.

South America has immense potential for mapping species distributions thanks to the extraordinary programme of gazetteer production for every South American country by R. A. Paynter (Harvard University, Cambridge, Massachusetts) and

M. A. Traylor (Field Museum of Natural History, Chicago). Each volume compiles all geographic localities in the ornithological literature, together with hundreds of unpublished localities represented in the world's major ornithological collections. Each entry lists the coordinates of the locality, elevation, habitat notes, and dates visited by the respective ornithological collector(s); see, e.g., the gazetteers by Paynter & Traylor (1991) for Brazil and by Paynter (1993, 1997) for Ecuador and Colombia. In the future, these and other gazetteers will permit the precise mapping of all South American species ranges for detailed biogeographical analyses, which so far have been based on less comprehensive datasets. When the complete distribution maps are available, it will be quite easy also to determine, for example, the coverage of the neotropical lowlands by museum samples and which museum collection contains the best representation of the bird fauna of a particular region in South America.

Zoogeographical aspects of the Amazonian bird fauna

I summarise below some results of my research based on studies of the birds preserved in the collections of several North American and European museums.

Areas of endemism

The ranges of many bird species and well-differentiated subspecies cluster in fairly restricted regions of the continents, characterising 'areas of endemism'. Other authors have designated such regions 'centres of endemism', 'distribution centres', 'core areas' and 'dispersal centres.' Six main areas of endemism are developed in Amazonia (Haffer 1969, 1974, 1978, Müller 1973, Cracraft 1985). Each of these areas is characterised by 10–50 species. By superimposing their ranges and contouring their numbers, areas of maximal overlap of breeding ranges of each species group are emphasised. These six areas of endemism are located in peripheral regions of Amazonia (Napo, Inambari, Imerí, Rondônia, Guiana and Belém). More widespread species inhabit increasingly larger distribution areas comprising two or more areas of endemism. Several groups of birds composed of geographically representative species characterising the several areas of endemism form conspicuous mosaic distribution patterns over all of Amazonia (e.g. *Pionopsitta* parrots, *Selenidera* toucanets, *Ramphastos* toucans and *Pipra* manakins).

In their global survey of endemism in birds, Stattersfield *et al.* (1998) identified only those areas of endemism ('endemic bird areas' or EBAs) which are characterised by at least two species with ranges of less than 50,000 km² each. They left unmapped other areas of endemism where the most restricted species have slightly larger ranges. This is the reason why in Amazonia only the Napo, Inambari and Imerí areas appear on their map (under slightly different names), whereas the very conspicuous areas of endemism of Guiana, Belém and Rondônia remained unidentified. This is not meant as a criticism but to point out the problem when a practical criterion (i.e. 50,000 km²) within the framework of conservation biology is used as a cut-off for biogeographic mapping in a huge lowland plain with no major barriers like Amazonia.

Contact zones between subspecies and species of birds

Many Amazonian birds meet and exclude each other geographically with or without hybridisation along sharply defined contact zones. These areas of contact represent major zones of biogeographic discontinuity in a continuous forest environment (Fig. 1, Table 1). Such pairs of taxa inhabit different levels of the forest; some prefer the canopy, others the middle levels and still others the understorey. Contact zones may or may not follow rivers at least for some distance.

As examples of conspicuous contact zones, I illustrate the distribution of three manakin species of the genus *Pipra* which inhabit forests near lowland rivers and are very common in many regions of Amazonia (Fig. 2). The males are mainly black, bright red and yellow; the females are inconspicuously green and similar to one another. Wire-tailed Manakin *P. filicauda* is slightly larger than the other two species; its tail feathers are elongated and their shafts project as long wire-like filaments (shorter in females). This species inhabits most of upper Amazonia (north to the coast of Venezuela), whereas Crimson-hooded Manakin *P. aureola* is found in the forests along the lower Amazon and Madeira Rivers as well as along the coastal lowlands of the Guianas. Band-tailed Manakin *P. fasciicauda* (with a white basal tail-band) occupies southern Amazonia and extended its range into north-eastern

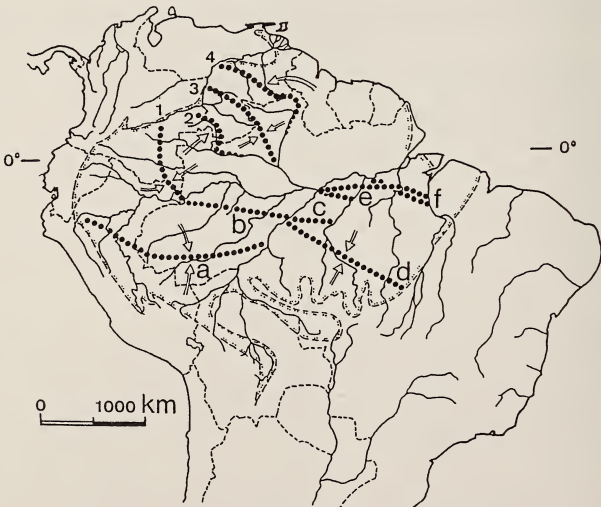


Fig. 1. Contact zones between selected Amazonian forest birds whose locations are independent of or variously displaced by river courses. For explanations of figures and letters see Table 1.

TABLE 1

Some species and subspecies of birds which form conspicuous contact zones in Amazonia (numbers and letters refer to Fig. 1).

I. North of the Amazon River; western representatives named first.			
1	Ramphastidae	<i>Selenidera reinwardtii</i>	<i>S. nattereri</i>
2	Formicariidae	<i>Gymnopithys leucaspis</i>	<i>G. rufigula</i>
3	Ramphastidae	<i>Ramphastos vitellinus culminatus</i>	<i>R. v. vitellinus</i>
		<i>Ramphastos tucanus cuvieri</i>	<i>R. t. tucanus</i>
	Picidae	<i>Veniliornis affinis</i>	<i>V. cassini</i>
4	Psittacidae	<i>Pionopsitta barrabandi</i>	<i>P. caica</i>
	Ramphastidae	<i>Pteroglossus pluricinctus</i>	<i>P. aracari</i>
		<i>Selenidera nattereri</i>	<i>S. culik</i>
	Picidae	<i>Celeus grammicus</i>	<i>C. undatus</i>
II. South of the Amazon River; the southern representatives are named first.			
a	Cuculidae	<i>Neomorphus geoffroyi</i>	<i>N. pucheranii</i>
	Pipridae	<i>Pipra fasciicauda</i>	<i>P. filicauda</i>
		<i>Pipra coronata exquisita</i> group	<i>P. c. coronata</i> group
b	Galbulidae	<i>Galbula tombacea</i>	<i>G. cyanescens</i>
c	Psittacidae	<i>Pionopsitta barrabandi</i>	<i>P. vulturina</i>
	Galbulidae	<i>Galbula rufoviridis</i>	<i>G. galbula</i>
	Capitonidae	<i>Capito dayi</i>	<i>C. brunneipectus</i>
	Ramphastidae	<i>Pteroglossus beauharnaesius</i>	<i>P. aracari</i>
	Cotingidae	<i>Xipholena punicea</i>	<i>X. lamellipennis</i>
d	Ramphastidae	<i>Ramphastos vitellinus pintoii</i>	<i>R. v. ariel</i>
	Dendrocolaptidae	<i>Xiphorhynchus elegans</i>	<i>X. spixii</i>
	Formicariidae	<i>Hylophylax poecilinota griseiventris</i>	<i>H. p. nigrigula</i>
	Pipridae	<i>Pipra nattereri</i>	<i>P. iris</i>
	Troglodytidae	<i>Thryothorus genibarbis</i>	<i>T. coraya</i>
e	Cotingidae	<i>Phoenicircus nigricollis</i>	<i>P. carnifex</i>
f	Pipridae	<i>Pipra fasciicauda</i>	<i>P. aureola</i>

and central Brazil. Where these species meet they replace each other geographically along sharply defined contact zones without (or very rarely) hybridising (parapatry). The contact zone between *P. aureola* and *P. fasciicauda* crosses the southern tributaries of the lower Amazon River at rightangles. The same is the case with the contact zone between *P. fasciicauda* and *P. filicauda* in upper Amazonia which crosses the Purús, Juruá and Ucayali Rivers at more or less rightangles. The situation along the upper Rio Juruá (Fig. 3) demonstrates the sharp replacement of these species in the uniformly distributed forests around the small village of Sobral where one male and three females of *filicauda* and two males of *fasciicauda* have been collected. Hybridisation does not seem to occur. To the south of Sobral, only *P. fasciicauda* is encountered in the forests to Taumaturgo and the Rio Tejo, a distance of 50 km (20



Fig. 2. Distribution of manakins of the *Pipra aureola* superspecies (males illustrated; plumage colour is yellow, red, orange and black). Locality records (symbols) refer to the following species: Crimson-hooded Manakin (*P. aureola*, open circles and horizontal hatching), Band-tailed Manakin (*P. fasciicauda*, solid circles and stippling), and Wire-tailed Manakin (*P. filicauda*, solid triangles and vertical dashes).

specimens in the Museu Paraense E. Goeldi, Belém, Pará). North of Sobral presumably only *P. filicauda* occurs. Details of the ecological relations between these two species will have to be determined through fieldwork around the village of Sobral.

Many contact zones cluster along the Amazon River and along the wide lower portions of some of its tributaries (Haffer 1978). However, the most important zoogeographical aspect of Amazonian contact zones is the fact that the locations of many other such zones are *independent* of river courses, crossing even the largest ones at rightangles, including the Amazon River itself. Examples of upper/lower Amazonian taxa whose contact zones in central Amazonia cross the middle or lower Amazon River from north to south are the following: Cobalt-winged Parakeet *Brotogeris cyanopectus* / Golden-winged Parakeet *B. chrysopterus*, 'Cuvier's Toucan'

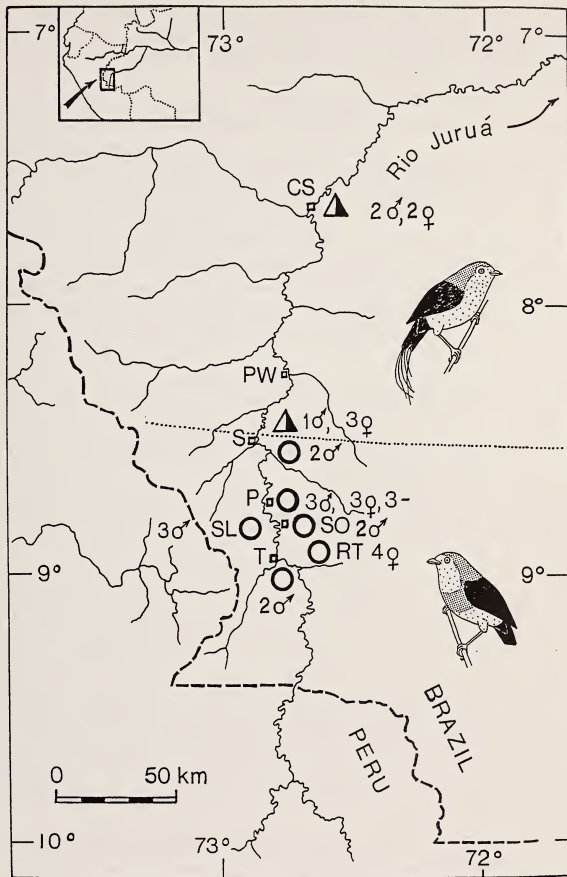


Fig. 3. Parapatric contact between Wire-tailed Manakin (*Pipra filicauda*, above and triangles) and Band-tailed Manakin (*P. fasciicauda*, below and circles) along the upper Rio Juruá in westernmost Brazil. Sketches illustrate adult males. Collecting localities from north to south are Cruzeiro do Sul (CS), Sobral (S; both species!), Porongaba (P), Igarapé São Luís (SL), Seringal Oriente (SO), Taumaturgo (T), and Rio Tejo (RT). PW Porto Valter. Dashed line follows border between Brazil and Peru.

Ramphastos t. cuvieri / 'Red-billed Toucan' *R. t. tucanus* and Rufous-bellied Euphonia *Euphonia rufiventris* / Golden-sided Euphonia *E. cayennensis*. The rich collections in several museums facilitated a detailed analysis of some of these contact zones (Haffer 1974, 1997).

I should clarify here the terminology I use. Geographically representative taxa of birds which meet without a separating barrier in an ecologically rather uniform area either hybridise more or less extensively along their contact zone or they exclude each other geographically with no (or only very restricted) hybridisation. In the former case these taxa represent subspecies of one biological species, whereas in the latter case they are differentiated at the species level. Such geographically representative species in contact are designated as 'parapatric' to distinguish them from sympatric (co-occurring) and allopatric (widely separated) species. Among the examples mentioned above, the representatives of *Brotojeris* and *Euphonia* are parapatric species, whereas those of the *Ramphastos* toucans hybridise extensively where they meet in central Amazonia. The intermediate populations are highly variable and composed exclusively of hybrid individuals; parental phenotypes are lacking. Under the biological species concept, *Ramphastos t. cuvieri* and *R. t. tucanus* are subspecies of the White-breasted Toucan *R. tucanus*. As mentioned above, the term 'parapatric' usually refers to species only, although some authors do speak of 'parapatric subspecies' in those cases where the connecting hybrid zone is very narrow (which is not the case in the toucans).

The members of parapatric species pairs probably compete ecologically and would extend their ranges across the contact zone but for the existence there of the competing ally (Haffer 1992). These contact zones are located in uniform (but complex) vegetation zones or in gradually changing habitat zones where, however, the ecological gradients are not steep enough to explain the abrupt replacement of the representatives. Each of them appears to be superior to the other in the respective area occupied. In the Eastern Andes of Peru, approximately two-thirds of the altitudinal distribution limits of bird species are due to ecological competition (Terborgh 1985). Competitive exclusion is one of the most important factors determining the composition of this rich bird fauna. The frequent occurrence of geographical exclusion of species along contact zones in the Amazonian lowlands as well as ecological exclusion of species within the rain forest through vertical stratification (Terborgh 1980) supports a similar interpretation of the importance of ecological competition for the determination of the regional composition of this rich tropical lowland avifauna.

Still to be determined for most or all instances of parapatric contact zones between bird species in Amazonia are:

- (1) What is the situation regarding the local distribution of the representative species? Do the contact zones remain stationary or do they fluctuate regionally or shift gradually in a certain direction?
- (2) In what manner is each zone of parapatry maintained, i.e. why do parapatric species not penetrate each other's ranges? Do agonistic behavioural responses

(interference competition) or resource preemption (exploitation competition) by their respective representatives prevent parapatric species from overlapping their ranges? Which mechanisms assure reproductive isolation of the species along their zone of contact? Does reinforcement of pre-mating isolating mechanisms and/or of ecological segregation between the species take place at the contact zones (i.e. will the two taxa gradually become more different in behaviour, calls, ecological preferences, etc.)?

(3) Why did parapatry originate in each case? Are the locations of contact zones the results of historical causes or of current ecological conditions? In instances of sympatry, these species might be expected to maintain interspecific territories or to occupy mutually exclusive patchy areas of varying extent.

(4) When did the parapatric species originate and when did they establish contact?

As examples of detailed taxonomic and zoogeographical analyses of contact zones with and without hybridisation of the taxa involved I cite the publications of Meise (1928, 1975), Short (1965), Remington (1968), Haffer (1977), and Panov (1989), all of which are based on extensive museum studies of bird collections.

Zoogeographical aspects of the avifauna of New Guinea

As in Amazonia, conspicuous areas of endemism and contact zones between birds are found in the lowlands of New Guinea. The bird faunas of the forested northern and southern lowlands are separated by the enormous 'wall' of the central mountain range extending for 2,000 km from the Geelvink Bay in the north-west to the south-eastern tip of the island. The following lowland regions are zoogeographically significant as areas of endemism (Stresemann 1936, Pratt 1982, Beehler *et al.* 1986): (1) the Vogelkop region at the north-western end of New Guinea; in northern New Guinea the basins (2) of the rivers Mamberano–Idenburg and (3) of the rivers Sepik–Ramu; (4) the lowlands of southern New Guinea. Examples of characteristic distribution patterns of lowland New Guinea birds are summarised in Fig. 4 and Table 2.

Many taxa of southern New Guinea extended their ranges westward beyond the Geelvink Bay into the Vogelkop region of NW New Guinea (Fig. 4/1B). In other cases the representatives of northern New Guinea reached the Vogelkop region first (Fig. 4/1C) or an endemic form exists in the latter area and three geographical representatives are in contact in the lowlands around the Geelvink Bay (Fig. 4/1A). This is the case, e.g., in the brush-turkeys *Talegalla* (Fig. 4/2) and the crowned-pigeons *Goura* (Fig. 4/3). The northern and southern taxa usually meet near the south-eastern end of the central mountain range where the northern or the southern form has surrounded the south-eastern tip of New Guinea or both meet there near Milne Bay. In several other cases the representatives are separated by a distributional gap.

The distributional ranges of the three *Talegalla* species inhabiting the Vogelkop region (Red-billed Brush-turkey *T. cuvieri*), northern New Guinea (Brown-collared

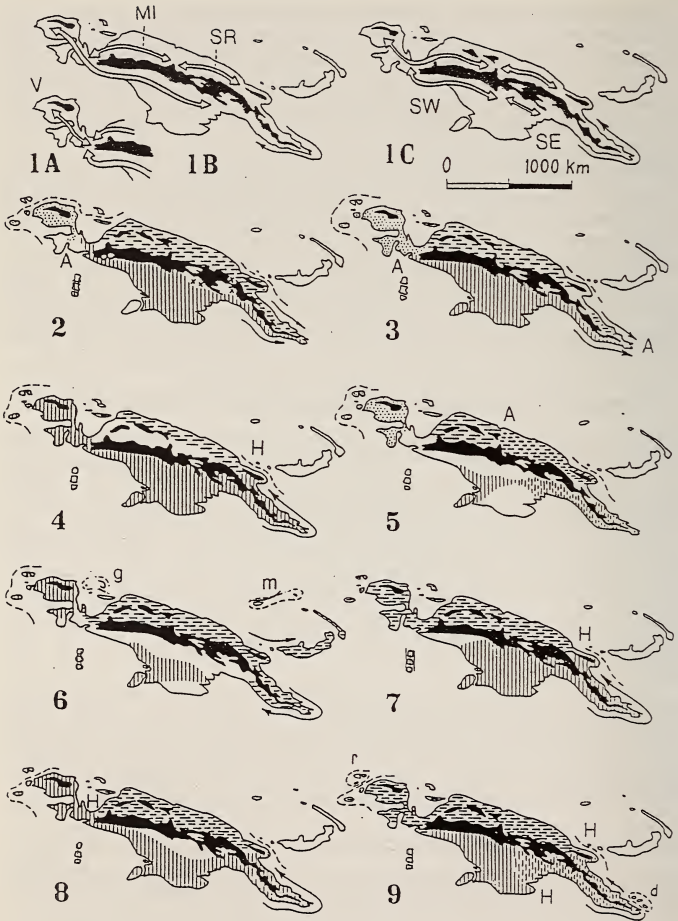


Fig. 4. Distribution patterns of selected species and subspecies of birds inhabiting the rainforests of the lowlands and lower montane levels in New Guinea, after Stresemann (1936) and Pratt (1982), with additional data. (Legend on page 17)

Brush-turkey *T. jobiensis*) and southern New Guinea (Black-billed Brush-turkey *T. fuscirostris*) are in contact in several areas but do not overlap. *T. cuvieri* and *T. fuscirostris* are in contact at the western end of the Snow Mountains where the former species inhabits the lower montane forests above the range of *T. fuscirostris* (Jones *et al.* 1995:117). In eastern New Guinea, *T. jobiensis* crossed low passes of the central mountain range in a southern direction and here also occurs locally in the lower montane forests above *T. fuscirostris* (Fig. 4/2). Obviously, the presence of *T. fuscirostris* prevents the southward advance of the two northern species into the lowland forests of southern New Guinea. The three *Goura* species replace one another geographically in a similar manner (with restricted hybridisation in the areas where they meet). In other birds where the geographical representatives are considered as subspecies, these taxa hybridise extensively along the contact zones or are assumed to do so.

Geographical variation

The individual and geographic variation of numerous bird species have been analysed for over one hundred years with methods that have become increasingly sophisticated in recent decades. These methods have been adequately reviewed by Selander (1971), Gould & Johnston (1972) and Baker (1985). I emphasise that detailed descriptions of local populations and artificial delimitation of subspecies cannot depict accurately the complex patterns of geographical variation in many wide-ranging species on continents. With sufficient specimen material available over a large area, computers can analyse regional trends statistically, and can generate isolines, contour maps, and trend-surface maps. In this way, regional patterns of character variation may be documented and analysed quantitatively, without *a priori* reference to subspecies

Legend to Fig. 4

Solid – mountains over 1000 m elevation. 1A–C Areas of endemism (open double arrows) as distribution centres of endemic species and subspecies (V Vogelkop, MI Mamberano–Idenburg region, SR Sepik–Ramu region, SW south-western lowland region, SE south-eastern lowland region). 1A Contact south of Geelvink Bay between endemic forms of the Vogelkop, the northern and southern lowlands; 1B Vogelkop and southern lowlands are inhabited by the same form (or group of subspecies) which established contact with the northern form at Geelvink Bay; 1C Vogelkop and northern lowlands are inhabited by the same form (or group of subspecies) which established contact with the southern form also at Geelvink Bay. Either the northern or the southern form extended its range around the south-eastern tip of New Guinea or both established contact near the tip itself (Milne Bay), e.g. map no. 3.

Symbols: A – geographical exclusion without hybridisation; H – hybridisation along the contact zone; stippled area – endemic form of the Vogelkop; dashed and hatched vertically – forms of the southern lowlands and, in some cases, of the Vogelkop; dashed horizontally – forms of the northern lowlands and, in some cases, of the Vogelkop.

Examples shown are: 2 *Talegalla*; note the occurrence of *T. cuvieri* on the southern slope of the Snow Mountains (two open circles) and of *T. jobiensis* on the southern slopes of the Central Mountains (x), 3 *Goura*, 4 *Lorius*, 5 *Psittaculirostris*, 6 *Micropsitta*, g *M. geelvinkiana*, m *M. meeki*, 7 *Geoffroyus*, 8 *Cicinnurus*, 9 *Paradisaea*, r *P. rubra*, d *P. decora*. For further details see text and Table 2.

TABLE 2

Characteristic species and subspecies of birds inhabiting the rainforests of the tropical lowlands and lower montane levels in New Guinea. Arrows indicate range extension. Numbers refer to the corresponding distribution maps in Figure 4.

	South (Fly River Platform)	North-west (Vogelkop)	North Mamberano– Idenburg	Sepik–Ramu
Megapodiidae	(2) <i>Talegalla fuscirostris</i>	→◀◀◀ <i>T. cuvieri</i> →	◀◀◀ <i>T. jobiensis</i>	
Columbidae	<i>Ptilinopus p. pulchellus</i>	————→	◀◀◀ <i>P. p. decorus</i>	
	<i>Ducula p. pinon</i>	————→▶▶	———— <i>D. p. jobiensis</i>	
	(3) <i>Goura scheepmakeri</i>	→▶▶ <i>G. cristata</i> →▶▶	———— <i>G. victoria</i>	
Psittacidae	<i>Chalcopsitta scintillata</i>	→▶▶ <i>C. atra</i> →▶▶	———— <i>C. duivenbodei</i>	
	(4) <i>Lorius l. lory</i> -group	————→▶▶	———— <i>L. l. jobiensis</i> -group	
	(5) <i>Psittaculirostris desmarestii</i> ¹	————→	◀◀◀ <i>P. salvadorii</i> →▶▶ <i>P. edwardsii</i>	
	(6) <i>Micropsitta keiensis</i>	————→▶▶	———— <i>M. pusio</i>	
	<i>Probosciger a. aterrimus</i> -group	————→▶▶	———— <i>P. a. stenolophus</i>	
	(7) <i>G. g. aruensis</i> -group		<i>Geoffroyus geoffroyi pucherani</i> -group	
Acanthizidae	<i>Gerygone p. palpebrosa</i> -group	————→▶▶	———— <i>G. p. wahnesi</i>	
Myiagridae	<i>Arses t. telescopthalmus</i> -group	————→▶▶	———— <i>A. t. insularis</i>	
Paradisaeidae	(8) <i>Cicinnurus r. regius</i> -group	————→▶▶	———— <i>C. r. coccineifrons</i> -group	
	(9) <i>Paradisaea apoda</i> + <i>P. raggiana</i>	▶▶———— <i>Paradisaea minor</i>		
Meliphagidae	<i>Philemon n. novaeguineae</i>	————→▶▶	———— <i>P. n. jobiensis</i>	
Dicaeidae	<i>Melanocharis n. nigra</i> -group	————→▶▶	———— <i>M. n. unicolor</i>	
Campephagidae	<i>L. leucomela</i>	————▶▶	———— <i>Lalage atrovirens</i>	
Orthonychidae	<i>E. c. nigricrissus</i>	————▶▶	———— <i>Eupetes c. caeruleus</i> -group	

¹ This species is composed of 2 subspecies on the west Papuan islands and 4 subspecies in western and southern New Guinea (in Fig. 4/5 stippled *desmaresti* + *intermedia*, hatched vertically *godmani*, dashed vertically *cervicalis*).

names (Haffer & Fitzpatrick 1985). Additional museum and field studies of intraspecific variation in birds are needed in order to document regional character changes along clines, across contact zones, and across various ecological gradients within the tropics.

The subspecies concept is most useful where applied to discrete, differentiated populations that are separated by distributional gaps like those found on islands. Within continuous populations inhabiting continental areas subspecies should be distinguished in only two situations: (1) at the ends of steep clines, if the two terminal populations show uniformity over a substantial portion of their ranges, and (2) where two or more wide-ranging populations show different, but in each case fairly uniform, character expression ('plateaus' on contour maps) connected by relatively narrow zones of character change.

Many examples of geographic variation in birds have been discussed by Mayr (1942, 1963), Zink & Remsen (1986) and, with particular reference to Palearctic birds, Voous (1947, 1949, 1950, 1953a,b) and Vaurie (1953–1964).

Arctic migrants

A recent example of an extensive quantitative study of the geographical variation of northern waders is the work of Engelmoer & Roselaar (1998) undertaken in the context of conservation work. Many wader species migrate in huge flocks along the East Atlantic flyway. For conservation purposes, it is important to determine approximately the composition of these flocks in relation to the different geographical origin of the breeding birds. Most of them congregate after breeding over widely dispersed areas in remote boreal and arctic regions as far apart as Greenland and the tundra of eastern Siberia where it is difficult to obtain population estimates. As long as morphometric and colour differences among breeding populations of the various species exist, quantitative estimates of the composition of migrating and wintering flocks are now possible based on a computer program ('Poscon') which determines the *posterior* probabilities and *confidence* intervals for a particular bird to belong to one of the differing breeding populations of its species. Based on their study of nearly 5,000 specimens in many museums, the authors analysed on a very thorough statistical basis the geographic variation of the breeding populations of 15 wader species of the Northern Hemisphere to provide a sound database for the continuing conservation effort with migrating and wintering wader populations in western Europe and in other parts of the world. Geographical variation is studied on the basis of standard measurements (lengths of wing, culmen, tarsus, tail, selected primary feathers, etc.) and scoring of the geographically variable colour of certain portions of the plumage like uppertail-coverts and axillaries in some species. The birds include such common migrants as Ringed Plover *Charadrius hiaticula*, Red Knot *Calidris canutus*, Sanderling *C. alba*, Dunlin *C. alpina*, Whimbrel *Numenius phaeopus*, Curlew *N. arquata*, Redshank *Tringa totanus* and Ruddy Turnstone *Arenaria interpres*.

Character geography within species groups

Comparative studies of the species and subspecies of a large genus or of a family permit historical and ecological analyses of various character states such as colour patterns, size, relative tail length and shape of tail, bill size and shape, voice, nests, nesting habits and their functional adaptations. Examples of such comparative evolutionary studies (of which many more are required) are those of Mayr & Moynihan (1946) on the flycatching Rufous Fantail *Rhipidura rufifrons* group in the Malay Archipelago and the Papuan region, and of Mayr & Amadon (1947) on the species of flowerpeckers, Dicaeidae, in these same regions. A similar analysis of the 20 species of drongo, Dicruridae, distributed in South-East Asia and the Malay Archipelago revealed that the characters of the more specialised species, such as large size, frontal crests, long tails, and modifications of the outermost tail feathers, have arisen independently in different branches of the family. Every character varies geographically and is correlated with such features of the environment as temperature and humidity. Double invasions of the same parental stock have led either to the existence of two sympatric species or to the formation of hybrid flocks (Mayr & Vaurie 1948:264-265). Snow (1954) published a similar treatment of trends in geographical variation in Palearctic members of the tits *Parus*. Other evolutionary trends among related allopatric species of the Neotropical Region are the increasing length of the central tail feathers in *Chiroxiphia* and of the uppertail-coverts in *Pharomachrus*.

Studies of the relations between wing and tail length in several groups of closely related species revealed certain trends whose functional interpretation is still open. In the series Brambling *Fringilla montifringilla*–European Chaffinch *F. c. coelebs* group–Chaffinch of NW Africa *F. c. spodiogenys* group–Canary Island Chaffinch *F. c. canariensis* [= *tintillon*] group, tail length increases as the wing becomes shorter and more rounded (Eck 1975). Tail length is only 70% of wing length in the Brambling and increases to 83% in the *F. c. canariensis* group. The underlying selection pressures may be linked to long-distance migration and 'island effect' (Grant 1979). With respect to size, the Blue Chaffinch *F. teydea* of pine forests in the mountains of Tenerife and Gran Canaria is an isometrically enlarged European Chaffinch. Wing and tail length decrease in the subspecies of the Sombre Tit *Parus lugubris* from the Balkan Peninsula east to northern Iran. Because small Père David's Tit *P. davidi* of south-western China, with bright cinnamon underparts, continues this trend of decrease in size, Eck (1980, 1988) considered this geographically isolated species as a representative and close relative of the western *P. lugubris*, pointing out that the plumage colour in *P. (L.) hyrcanus* of northern Iran (underparts tinged rusty) is somewhat intermediate. The Great Tits of the *Parus major* complex have a wing length of approximately 65–80 mm; the tail is relatively longer and more graduated in the *bokharensis* group of Middle Asia than in the other subspecies groups (Eck 1977).

Geographical variation in sexual dimorphism

In several species of birds females show stronger geographical variation than males ('heterogynism': Hellmayr 1929). This has been observed in South American antbirds, *Thamnophilidae*, in which the males have a non-variable black plumage while the colouration of the females is geographically variable shades of brown. Other examples of heterogynism are White-shouldered Fairywren *Malurus alboscapulatus* (Mayr & Rand 1935) and Sulawesi Cuckooshrike *Malurus alboscapulatus* (Mayr & Rand 1935) and Moluccan Greybird *Coracina morio* (Stresemann 1939). It remains unknown how widespread heterogynism is among birds.

A related topic is the geographically varying degree of sexual dimorphism. On small oceanic islands, some birds show reduced conspicuousness and sexual dimorphism compared with their mainland relatives, probably because there are fewer species on the islands and the problems of species recognition are reduced, resulting in a reduction of sexual dimorphism. A latitudinal gradient of sexual dimorphism involves the New World warblers, *Parulidae*, and New World orioles, *Icteridae*. Tropical species tend to be sexually monomorphic and conspicuous, whereas north temperate species tend to be sexually dimorphic (Hamilton 1961). Nesting habits also influence the degree of sexual dimorphism. The females of hole-nesting birds, such as rollers, kingfishers and parrots, are frequently as colourful as their males, because they need no protection through adaptive (camouflage) colouration while sitting on the nest.

Three particularly conspicuous examples of geographical variation in sexual dimorphism are the highly polytypic Golden Whistler *Pachycephala pectoralis* of the Malay Archipelago, Papuan and Australian regions (Mayr 1932, Galbraith 1956), Scarlet Robin *Petroica multicolor* of the islands in the south-western Pacific Ocean (Mayr 1942:48) and the *Pomarea* 'flycatchers' of the Marquesas Islands (Murphy 1938). A genetic drift hypothesis may account for the origin of geographic variation in sexual dimorphism in birds (Peterson 1996).

Geographical variation in polymorphism

In most polymorphic species with discontinuous colour phases there is no evidence for selective mating or any other advantage of the morphs (Mayr 1942:75). In some instances polymorphism varies geographically, the percentages of morphs in the populations changing over large distances, e.g. in the Pacific Reef-heron *Egretta sacra*, Grey Goshawk *Accipiter novaehollandiae* and Papuan Lorikeet *Charmosyna papou* (reviewed by Huxley 1955). In some cases, geographical gradients in polymorphism may be linked to hybridisation along secondary contact zones of previously separated (monomorphic) populations. Subsequent regional introgression may have led to the development of polymorphism, e.g. in the Black Bulbul *Hypsipetes leucocephalus* (Mayr 1941, 1942:83) and in two pairs of wheatear species, Black-eared Wheatear *Oenanthe hispanica*/Pied Wheatear *O. pleschanka* (Haffer 1977) and Variable Wheatear *O. picata*/*O. opistholeuca* (Panov 1992). Huxley's

conclusion is still valid: 'The time seems ripe for a detailed survey of the incidence of colour- and pattern-morphism in birds'.

Conceptual contributions of systematists

Conceptual contributions of systematists to the biological sciences through their museum studies of animal collections include the theory of geographical speciation, the principle of population thinking and the interpretation of the gradualness of evolution (Mayr 1973, 1980). These topics will be briefly discussed below.

Geographical speciation

Beginning with Leopold von Buch, Charles Darwin and Alfred R. Wallace during the first half of the nineteenth century a steadily growing number of systematists advocated the theory of geographical speciation from small isolated populations. This theory combines two seemingly incompatible aspects, namely (1) gradual evolutionary differentiation of a separated population and (2) the existence of bridgeless gaps between coexisting species after the completion of isolating mechanisms (Mayr 1942, 1963). The zoogeographical phenomena discussed above, like areas of endemism and the occurrence of contact zones in Amazonia and in other regions of the world, may be interpreted in terms of the theory of geographical speciation. Repeated climatic-vegetational fluctuations during the last several million years probably led to the fragmentation and differentiation of the vegetation zones and their contained faunas, leading to the development of areas of endemism. As climatic conditions changed, the more or less separated faunas were rejoined, leading to the overlap and sympatry of ecologically fully compatible species and to the formation of the contact zones between representative taxa which had reached various intermediate stages of the speciation process during their geographical separation (Mayr 1942, 1963, Haffer 1974, 1997, Haffer & Prance 2001).

Population thinking

Ornithologists of the mid-nineteenth century discovered, when collecting 'series' (population samples) of specimens of one species from certain localities and from different regions, that no two specimens were ever completely alike. These are the phenomena of individual and geographical variation, respectively. For example, H. Schlegel in the Netherlands and J. H. Blasius in Germany, as well as the ornithologists around S. F. Baird of the Smithsonian Institution in Washington, D.C., made great efforts to assemble, from the 1850s to the 1880s, series of specimens of each species to determine the range of variation, publishing detailed lists of all birds examined with information on sex, locality, measurements and colour characters. These workers emphasised the occurrence of individual variation of local populations and of geographically representative forms (subspecies) delineating polytypic species. Many of these and other ornithologists studied variation even though they held typological (essentialistic) views, assuming that an internal type or essence maintains the integrity

of each constant species and that variation is no more than an imperfect manifestation of its eternal type.

However, the studies of the ornithologists mentioned above prepared the ground for the development of 'population thinking' (Mayr 1959, 1982:46). Under this evolutionary principle individual and geographical variation are real and represent important phenomena of the natural world. Geographical variation of isolated populations may transcend species limits and lead to the origin of new species. Species possess no eternal integrity, and types in the sense of essentialism are abstractions. Basic concepts like natural selection acting on populations composed of varying individuals are meaningless for typologists. The replacement of typological thinking by population thinking through the research of museum workers is perhaps the greatest conceptual revolution that has taken place in biology. From systematics it was brought into genetics by researchers who had either been trained as systematists or had worked closely with systematists (Mayr 1963:5, 1973).

Gradualness of evolution

During the early twentieth century, museum systematists endeavoured to demonstrate, through detailed analyses of geographic variation of numerous species, that evolution proceeds gradually, as Darwin had postulated, rather than through 'saltations' (jumps), as the Mendelists assumed during that time. Rensch (1929) showed that all species characters vary geographically and that extreme geographical subspecies may differ morphologically more from one another than many good sympatric species. This observation made the interpretation of gradual evolution much more probable than a saltational course of microevolution.

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